# The Biology of Polyporus squamosus, Huds., a Timber-destroying Fungus.

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BY

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# THE BIOLOGY OF POLYPORUS SQUAMOSUS, HUDS., A TIMBER-DESTROYING FUNGUS.

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With Plates V—IX and 6 Text Figures.

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## INTRODUCTION.

### General Remarks upon the Destruction of Wood.

Millions of tons of wood are produced every year in the forests of the world. Observation, however, tells us that the sum-total of wood upon the surface of the earth remains fairly constant from year to year and from century to century. We must, therefore, conclude that there are destructive agencies at work by which millions of tons of wood are destroyed annually. Regarded in this light the problem of what these destructive agencies are, and how they act, becomes of general scientific and economic interest.

The balance between the amount of wood formed by trees and

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that destroyed in a given period of time, such as a century, has not always been kept. An excess production of wood led to the formation of the Coal Measures. There is no reason to suppose that the assimilatory activity of trees during the Carboniferous Period was any greater than now, if similar climates be taken into account. The accumulation of wood seems to have been due to the geological conditions having been unfavourable to the destructive agencies, and in particular to fungi. The dead parts of trees, which are deposited on the floors of our European forests, are kept constantly moist or wet, while yet being mixed with plenty of air. Under these conditions the wood-destroying fungi flourish. During the Carboniferous Period, however, the dead leaves, twigs, and trees, upon falling, seem to have been quickly plunged beneath free water, and thus to have become thoroughly soaked. They further appear to have been carried by streams into salt lagoons [1] or lakes, and there to have been finally deposited. At the present day such conditions appear to be very unfavourable to the wood-destroying fungi. Wooden piles, submerged beneath either fresh or salt water, remain long, if not entirely, preserved from the inroads of these organisms. Thus the piles in the lake-dwellings of Switzerland and Ireland have lasted for centuries. When the piles of Old London Bridge [2] were taken up they were found to be sound after six hundred and fifty years of use. Complete saturation of wood with water, which now preserves timber from the inroads of fungi, was in all probability just as unfavourable to these organisms in the Carboniferous Period. The accumulation of the Coal Measures may thus perhaps in part be accounted for.

Among the agents at present at work in destroying wood, animals will be first shortly considered.

Almost all the higher forms leave wood untouched, if for no other reason, because its mechanical resistance defies their teeth. Elephants, with their huge grinders, tear down branches, pound them up, and thus feed on woody fibre.[3] A few rodents have the habit of gnawing wood, partly for the purpose of making burrows in which to live or hide, and partly in order to obtain food. The enormous annual destruction of wood and indeed of standing timber by fire through the agency of man is of course a matter of general knowledge.

Certain Crustacea of the group Malacostraca, *e.g.*, *Chelura terebrans*,[4] bore into wood piles, and thus weaken them. Some Molluscs of the group Lamellibranchiata, *e.g.*, *Teredo navalis*, the "ship-worm,"

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[1] Geikie, Text-book of Geology, 3rd ed., p. 805.
[2] G. S. Boulger, Wood, 1902, p. 254.
[3] Hutchinson, Extinct Monsters, p. 211.
[4] R. Hertwig, Lehrbuch d. Zoologie, 4te Augl., p. 386.

have the same habit. By boring into piles the animal has been the cause of the breaking of certain dams in Holland,[1] with the loss of many human lives.

It is well known that many insects bore into wood. According to Drummond,[2] in certain parts of tropical Africa not a stick falls to the ground but is immediately converted into powder by the activity of the Termites or so-called White Ants. The true Ants, too, sometimes make their living rooms in wood. This the writer has observed near Munich, where old stumps are frequently thus inhabited.

Numerous species of Coleoptera inhabit wood. One of the best known cases is that of *Anobium striatum*, which often destroys furniture. This insect flourishes in air-dry timber, where it is practically free from all competitors. No fungus could grow under such conditions. It seems probable that *Anobium*, as well as certain Mites that live on dried plant specimens, obtain the water necessary for the structure of their tissues by splitting up carbohydrates,[3] such as cellulose and starch.

It is certain that many insects live upon the wood into which they burrow. They first pulverise it. Whether or not they merely dissolve out the cell-contents, such as starch and proteids contained in the medullary rays and wood parenchyma cells by means of appropriate enzymes, leaving the actual cell-membranes chemically unaltered, has, so far as the writer knows, not yet been definitely ascertained. I examined the dust produced by *Anobium striatum* in a thick piece of stem of the Sugar-cane. The dust was found to consist of faeces which were mainly made up of broken cell-walls, mixed, however, with many starch grains. The cell-walls were still lignified, and no free cellulose could be detected. The usual tests with phloroglucin and hydrochloric acid, with chlorzinc iodine and with iodine and sulphuric acid, were employed. Proof was thus obtained that lignified membranes can pass through the alimentary canal of *Anobium* without becoming delignified.

We may now consider the vegetable organisms which destroy wood.

Bacteria are the cause of the breaking down of so many organic substances, that we might well expect that they are also concerned in the destruction of wood. They are indeed suspected of bringing about the decay of wood in the roots of *Pinus sylvestris* suffering from the disease known as "Wurzelfäule." As yet, however, no wood-destroy-

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[1] R. Hertwig, *loc. cit.*, p. 328; *vide* also Hedley, Austral. Ass. Adv. Sci., 1901, p. 237.

[2] H. Drummond, Tropical Africa.

[3] This method of obtaining moisture has already been suggested by Massart in the case of desert insects which live on dry dung. Le Desert, Bruxelles, 1899, p. 15.

ing bacteria have been isolated. Bacteria which destroy unlignified membranes, those consisting of cellulose, are very wide-spread in nature and can be obtained from any soil containing humus, or pond where vegetable matter is decomposing.[1] In some cultures which I made with these bacteria,[2] the cellulose fibres of filter-paper were rapidly destroyed. On the other hand spiral vessels and pitted ducts present in the vascular bundles of some succulent leaves and stems, which had also been introduced into the cultures, survived the action of the bacteria apparently unaltered. This observation makes it doubtful whether the cellulose-destroying bacteria are also able to break down lignified membranes. The whole question of the relationship of bacteria to the decay of wood certainly requires investigation.

The chief agency at work in destroying wood is undoubtedly the Fungi. Of these the groups concerned are the Ascomycetes and the Basidiomycetes.

The Ascomycetes rarely do much damage to the wood in bulk, such as tree-trunks or thick branches. They are numerous, however, upon twigs and the surface of wood. They require a comparatively small amount of food to produce their small fruit-bodies.

The Basidiomycetes are the most active destroyers of wood. The lower forms have comparatively simple fruit-bodies, and are often found on small branches. The higher forms, however, have more complex, and, as a rule, much more massive fruit-bodies. They thus require a comparatively large amount of food to complete their development. When wood is the food, this is obtained by acting with enzymes upon the substance of thick branches and tree-trunks. In this manner the Basidiomycetes remove most of the wood which falls to the floor of our forests.

It is admitted that if timber be kept perfectly dry, or submerged beneath water, it will resist decay for an indefinite period. It was formerly thought that alternate exposure to air and water was sufficient, *per se*, to bring about the decay of wood. There is, however, no evidence that such is the case in the absence of living organisms.

## LITERATURE.

The causes which lead to the decay of wood were elucidated toward the latter end of the nineteenth century.

Theodore Hartig was the first to scientifically investigate the decay of wood, and published the results of his work in 1833 in a paper entitled "Abhandlung über die Verwandlung der polycotyledonischen Pflanzenzelle in Pilz- und Schwamm-Gebilde und der daraus hervorge-

[1] Omelianski, Ref. in Chem. Centralbl., 1898, Bd. i, p. 269.

[2] Buller, Die Wirkung von Bakterien auf tote Zellen. Dissertation. Leipzig, 1899, p 20.

henden sogenannten Fäulniss des Holzes."[1] Hartig's views of the red-rot of trees were as follows:—As a tree passes a certain age the functions of its parts begin to be lost, bringing about the decay of the wood. This may, however, happen earlier in consequence of unfavourable external conditions. The first step in decay is the breaking up of the contents or membranes of the wood cells into tiny balls or monads. These monads gradually form rows and fuse, thus becoming converted into fungus hyphae. These hyphae can then grow and infect wood which is sound and cause it to rot. Hartig called the fungus by the somewhat fanciful name of *Nyctomyces* (Nachtfaser), as an indication that the hyphae originated in deepest darkness. Although Hartig shared the views of his time, and explained the presence of the fungus by spontaneous generation, he discovered facts which made him hesitate in this conclusion. Having observed the fruit-body of a *Polyporus* upon the outside of a rotten tree, in which he could make out the *Nyctomyces* hyphae, he asked himself the question whether the fruit-body had not been produced by the *Nyctomyces*. He failed to find the connecting hyphae, the presence of which would, he said, entirely alter his views upon the origin of the *Nyctomyces*. Hartig's work was, however, of considerable value, for it added to our knowledge the fact that the decay of wood is usually connected with the presence of fungus hyphae.

The origin of the hyphae in decaying wood from spores produced by fruit-bodies became clear from the researches of de Bary, Tulasne and others upon plant diseases.

Schlacht[2] investigated the changes brought about by fungi in dead plant cells. He observed the disappearance of starch, protoplasm and cell-walls, paying particular attention to the passage of hyphae through cell-walls and to their corrosion. Owing to the absence of fruit-bodies, Schlacht failed to identify the fungi which he saw.

In 1866 Willkomm, in his "Microscopische Feinde des Waldes," gave an account of some investigations upon Red Rot and White Rot. He observed different kinds of hyphae in rotting wood, but failed to connect them with the fruit-bodies of Basidiomycetes. He added little that was new upon the subject. His work serves, however, to show how incompletely the decay of wood was then understood.

In 1878 appeared Robert Hartig's work called "Zersetzungserscheinungen des Holzes."[3] It was provided with many excellent illustrations, and threw a flood of light upon the decay of wood. The fungi concerned and their method of action were described in detail.

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[1] T. Hartig, Berlin.

[2] Hermann Schlacht, Jahrbücher f. wiss. Bot., 1863, Bd. 3, p. 442.

[3] Berlin, 1878.

The account included *Trametes radiciperda*, *T. pini*, *Polyporus fulvus* (*Hartigii*), *P. vaporarius*, *P. mollis*, *P. borealis* and *Agaricus melleus* upon the Coniferae, and *Hydnum diversidens*, *Thelephora perdix* (*Stereum frustulosum*), *Polyporus sulphureus*, *P. igniarius*, *P. dryadeus* and *Stereum hirsutum* upon the Oak. Hartig showed that each fungus has a specific action upon wood, so that it is often possible by macroscopic inspection of a piece of wood to determine the fungus concerned in the decay, even in the absence of fruit-bodies. Great attention was paid to the corrosion of cell-walls and their dissolution.

Several other publications[1] of Hartig are more or less devoted to the decay of wood. The chief is his monograph on *Merulius lacrimans*,[2] the so-called Dry Rot fungus.

Marshall Ward has written a note upon "*Penicillium* as a wood-destroying fungus."[3] In a paper "On the Biology of *Stereum hirsutum*,"[4] he describes pure cultures of the fungus from the spore to the fruit-body, and gives an account of the changes it produces in wood. In the first number of this journal I have given an account of the destruction of wooden paving blocks in the streets of Birmingham[5] by *Lentinus lepideus*.

A pure culture of a wood-destroying fungus—*Collybia velutipes*—was made by Constantin and Matruchot,[6] and later also by Biffen.[7] In an excellent paper by Falck[8] a description with photographs is given of pure cultures of *Collybia velutipes*, *Hypholoma fasciculare* and *Phlebia merismoides*, three Agarics, which live on dead wood. The fruit-bodies were obtained from oidia, which are produced by the breaking up of the mycelium grown in pure cultures from spores.

In a paper "On the Biology of *Bulgaria polymorpha*, Wett." Biffen[9] has described the delignification of the cell-walls and removal of the middle lamellae from the wood of the Oak by the fungus.

In America, von Schrenk[10] has recently published a number of

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[1] Wichtige Krankheiten der Waldbäume. Berlin, 1874; Unters. aus d. Forst-bot. Institut zu München, 1883, iii; Allg. Forst. und Jagd-Zeitung, 1887; Forstl-naturw. Zeitschrift, 1893, p. 57; Centralb. für das gesammte Forstwesen, Heft 6, 1900; Pflanzenkrankheiten. Berlin, 1900, pp. 165-208.

[2] Hartig, Der ächte Hausschwamn *(Merulius lacrimans)*, Berlin, 1885.

[3] Marshall Ward, Ann. of Botany, 1898, vol. xii.

[4] Marshall Ward, Phil. Trans. Roy. Soc., 1897, vol. 189, p. 123.

[5] Buller, Journ. Econ. Biol., 1905, vol. i, p. 2.

[6] Constantin and Matruchot, Comptes Rend., 1894, vol. 119, p. 752.

[7] Biffen, Journ. Linn. Soc., 1899, vol. xxxiv, pp. 147-162.

[8] Richard Falck, Beitr. z Biol. d. Pflanzen-Cohn, 1902, Bd. viii, p. 307.

[9] Biffen, Ann. of Botany, 1901, vol xv, p. 119.

[10] Von Schrenk, U.S. Dept. of Agric., Bull. no. 25, 1900; ibid., no. 21, 1900; 12th Ann. Rpt. Missouri Bot. Gardens, 1902; Journ. Western Soc. Engineers, 1901; Yearbook Dept. of Agric. for 1900; U.S. Dept. of Agric., Bull. no. 14, 1902; ibid., no. 32, 1903; ibid., no. 36, 1903.

papers upon the destruction of wood and the diseases of forest trees. His work is of practical as well as scientific interest.

Czapek[1] has made an important contribution to our knowledge of the enzymes of the wood-destroying fungi. He has extracted an enzyme from *Merulius lacrimans* which brings about the delignification of wood. He regards a lignified cell-wall as an ester of cellulose and hadromal,[2] which can be split up into its constituents by the enzyme which he has named hadromase. The cellulose can then be decomposed by cytase.

## The Present Research.

Hartig's work was limited to the destruction of the Oak and Coniferae of the German forests. At his suggestion I have made an investigation into the destruction of the wood of the Sycamore (*Acer pseudoplatanus*). He kindly placed at my disposal a quantity of material which he had collected, illustrating the decay as caused by *Polyporus squamosus*, *Fomes vegetus*, and *Agaricus melleus*. The present paper is devoted to the first-named fungus.

The work was commenced in 1900, during the term of an 1851 Exhibition Scholarship at the Forst-botanisches Institut at Munich, here the anatomy and chemistry of the rotten wood was completed. The life-history of the fungus was studied at the University of Birmingham.

I am much indebted to the late Professor Robert Hartig for the kind interest he took in the research, for providing me with the necessary material, and for the liberal manner in which he gave me the advantages of criticism based upon a life-long and unique experience of forestry and plant-pathology.

# POLYPORUS SQUAMOSUS, Huds.

## General Remarks.

*Polyporus squamosus*, the Great Scaly Polyporus, or Saddle-Back fungus, is one of the best known of the tree-destroying fungi. Its large ochraceous fruit-bodies, checkered with brown scales above, are frequently to be seen projecting as brackets, either singly or in groups, from branches or the trunks of trees in woods, parks and gardens (Fig. A). The fungus destroys a large number of ornamental trees,

[1] Czapek, Ber. d. D. bot. Gesell., 1899, Bd. xviii, p. 166.
[2] Czapek, Zeitschr. fur physiologische Chemie, 1899, Bd. xxvii, p. 14.

and should therefore be of interest to all who have the care of them.

Fig. A.—*Ulmus montana*, with five fruit-bodies of *Polyporus squamosus* growing out from a large wound surface where a great branch has been broken off. The top fruit-body has a vertical central stipe in middle of pileus. About $\frac{1}{20}$ nat. size.

The fungus is common throughout Europe, and is recorded as

having been found upon an Elm in the State of New York.[1] It also occurs in Minnesota.

During a two years' residence at Munich I had frequent opportunity of observing the fruit-bodies. In 1901 a series of fine old Chestnuts and Sycamores were cut down in the Hof-garten, owing to the majority having suffered from fungus attacks. In three cases fruit-bodies demonstrated the presence of *Polyporus squamosus*. During July, 1901, four of the Red Chestnut trees in front of the Wittelsbacher Palast were bearing fruit-bodies simultaneously. In the Englisher Garten I found two Wych Elms and an Ash in a similar condition.

In England, in the course of two years, I noticed the fruit-bodies in the suburbs of Birmingham twice upon the Wych Elm, once upon the Beech, once upon the Sycamore, and once at the Botanical Gardens on *Pirus vestita*. I have also found the fungus at Sutton Coldfield, Havant, Banbury, Oxford, and on the Elms at the Backs at Cambridge. A number of specimens have been brought to me from various places by friends. During the summer of 1905 I watched the development of five sets of fruit-bodies on logs in the Experimental Greenhouse of the Birmingham University. I here wish to express my thanks to Professor Hillhouse for kindly placing the resources of the Greenhouse at my disposal.

*Polyporus squamosus*, to the best of my knowledge, has never been recorded upon any of the Coniferae. Otherwise it is not very particular in choice of its host, for various authors record it upon the following trees: *Acer pseudoplatanus*, *A. platanoides*, *A. negundo*, *A. dasycarpum*; *Pirus communis*, *P. ancuparia*, *P. vestita*; *Quercus*; *Ulmus*; *Corylus*; *Juglans regia*; *Tilia*; *Salix*; *Fraxinus*; *Betula* and *Aesculus*.

From my own experience, and from the accounts of others communicated to me, I estimate the numbers of trees in Europe at the present moment infected with *P. squamosus* as being not less than several hundred thousands. The damage wrought to standing timber is, in the aggregate, not inconsiderable, as may be gathered from the following instance. A forester in charge of the Englisher Garten at Munich informed me that a fine old Wych Elm, some 3ft. 6in. in diameter near the base, which was growing there, was, if sound, worth 400 marks for its timber. The tree, however, was badly attacked by *Polyporus squamosus*, huge brackets projecting from the trunk in several places. As the tree was dying it was cut down. The bole was found within to be very rotten, so that its wood was only rendered fit for firewood.

The fruit-bodies of *Polyporus squamosus* are the largest among

[1] Saccardo, Sylloge Fungorum, Bd. vi, p. 100.

British fungi. Although I have found specimens less than four inches across, yet such as are one foot in diameter are frequent. I obtained

Fig. B.—Fruit-body of *Polyporus squamosus* nearly full-grown; upper surface covered with brown scales. The full length of the stipe is photographed. $\frac{1}{8}$ nat. size.

one, not fully developed, fifteen inches across, the top being nearly circular (Figs. B and C). During the summer of 1905 I gathered a per-

fect specimen, two feet, two inches across, and having a perimeter of six feet three inches. It weighed approximately $6\frac{1}{2}$ lbs. The fruit-

Fig. C.—Under surface of fruit-body of *Polyporus squamosus* nearly full-grown, showing the pores of the hymenial tubes and the reticulations on the stipe. The fruit-body was photographed immediately after it was cut; the curling over of the edge of the pileus is quite natural. $\frac{1}{3}$ nat. size.

bodies are also remarkable for their rapid rate of growth. If the

weather is warm brackets 6-10 inches in diameter may complete their development in about a fortnight. At Munich, in the month of August, I observed five fruit-bodies reach their full extension in about ten days. About the same length of time was also required by specimens grown in the Experimental Greenhouse.

Greville[1] says: "My esteemed friend, Dr. Hooker, relates an instance given him by Mr. Hopkirk of one which measured 7ft. 5in. in circumference, and weighed, after having been cut four days, 34 lbs. avoirdupois. It was only four weeks attaining the above size, gaining thus an acquisition of above 1 lb. 3 oz. in the day." I cannot help being sceptical with regard to these figures, which after all are given at third hand. As already stated, the fruit-body which I found last summer was 6ft. 3in. in circumference, and weighed 6½ lbs., whilst Mr. Hopkirk's specimen, which was a little larger, 7ft. 5in. in circumference, is said to have weighed 34 lbs. The size of the fruit-body may have been correctly given, but if so it seems to me only reasonable to suppose that the weight has been magnified about four-fold. Mr. Hopkirk's fungus seems to have grown most rapidly as the account of it was passed on from one observer to another.

The fruit-bodies are annual. They are produced from May till September. In the Midlands of England they are especially abundant in July. If developing in warm sunny weather insects soon find them out, causing them to become infested with larvae often before reaching maturity. Fruit-bodies may thus become putrescent and fall within a few days or weeks after being fully formed. This is particularly the case with large fleshy forms. As soon as they are fully extended the fall of spores from the hymenial tubes begins. The spore-fall was found in the case of specimens grown in the Greenhouse to last from about five days to a fortnight, according to the size of the fruit-bodies and the conditions of their development. After the spore-fall the fruit-bodies die almost immediately. Sometimes the dead fruit-bodies hang on the tree throughout the winter, and occasionally for years. This is more especially true for the smaller fruit-bodies produced late in the year. Slugs are fond of the young fruit-bodies, and often damage them considerably.

At first the fruit-bodies are soft and juicy, and in this state are good to eat, although even then they are somewhat leathery. The flavour is distinctly pleasant, but in my opinion not equal to that of the Mushroom, *Agaricus ostreatus*, or of *Coprinus comatus*. Upon getting older and dryer they gradually become very tough. To such an extent is this the case that dried pieces of the fungus have a surface like that of the finest leather, and in some districts are used as razor-

[1] Greville, Cryptogamic Flora, vol. iv, p. 207.

strops. On this account the fungus has been called in Germany the "Herrenschwamm." The smell of a fresh fruit-body is not unpleasant. Dried specimens, however, usually have a strong and disagreeable odour.

The excretion of water from the hymenial surface which is characteristic of certain Polyporei, notably *Merulius lacrimans* and *Polyporus dryadeus*, also takes place in the case of *Polyporus squamosus*. I observed on two different mornings a large number of drops of water hanging from the mouths of the hymenial tubes of some young fruit-bodies growing near the ground on *Pyrus vestita*, and confirmed these observations on specimens at Cambridge (Pl. IX, fig. 47, *g*). In the laboratory drops only appeared when the air was very moist.

*Polyporus squamosus* is usually a wound-parasite. Its spores in all probability germinate upon the wound surfaces of broken branches, the mycelium thus making its way directly into the wood. There is no evidence to show that an uninjured tree can become infected. The bark appears to resist penetration by any germ-tubes from without. So far as my experience has gone fruit-bodies of the fungus are always to be found actually upon or near obvious wound-surfaces where the wood has been laid bare, so that germ-tubes could have made an entrance directly into it (Fig. A). As trees get older they become more and more liable to have wood surfaces exposed owing to damage by wind, snow, lightning and frost, etc. The older trees become, therefore, the more likely they are to be infected by wood-destroying fungi.

In parks and gardens, for various reasons, large branches are frequently cut from Horse Chestnut trees, Sycamores, Beeches, etc., and thus admirable wound surfaces prepared, by which *Polyporus squamosus* (or any other wood-destroying fungi) may make its way into the trunk. In many of the cases that I have observed infection has almost certainly taken place in this way, fruit-bodies having subsequently appeared on the wound surfaces. When branches are sawn off valuable ornamental trees, the exposed surfaces left ought to be at once creosoted or treated with some other antiseptic to prevent the germination of spores. If this is not done there is always great risk that wood-destroying fungi will enter the trees and gradually cause their decay or death.

When the mycelium of *Polyporus squamosus* has entered a large branch, guided by the cells, it makes its way gradually to the centre of the tree-trunk (Pl. V, fig. 7), and then spreads upwards and downwards in it, causing it to rot from within outwards. The fungus spreads very gradually to the periphery, thus reducing every year the amount of sound wood. The conduction of water up the stem appears to be slowly interfered with. At any rate one notices a gradual dying

away of the branches of an infected tree. Finally the whole tree may succumb.

When a tree has been killed by *Polyporus squamosus* the fungus can still continue its annual production of fruit-bodies. This I observed in the case of *Pyrus vestita*. The fungus can then be regarded as a saprophyte. When such a dead or half-dead tree is cut down fruit-bodies of the fungus may be produced on the stump. I have observed them on a number of such stumps, and also on a flag-post near the ground. The infection probably took place when the trees concerned were living. There seems, however, no reason why, under favourable conditions, dead wood should not be infected by means of spores and the fungus propagate itself as a pure saprophyte. As a rule, among the tree-destroying fungi there is, as in the case of *Polyporus squamosus*, no hard and fast line between parasitism and saprophytism.

## The Spores and their Germination.

The spores (Pl. VI, fig. 8) are unicellular, elliptical and colourless. They measure 12-14 $\mu$ long and 5-6 $\mu$ broad. The protoplasm, which can be seen through the spore-wall, usually contains a distinct vacuole near the centre.

The spores are very numerous. Their number was calculated in the following manner. A fresh fruit-body, which had just reached maturity, was removed from a tree and placed with pores downwards upon a piece of smooth brown paper. Upon this the spores gradually fell down from the hymenial tubes, forming small white heaps Pl. V, fig. 1). A square centimetre of the paper, on which were 26 heaps of spores, deposited from as many tubes, was then carefully cut out and stirred up with 25 cc. of water. In this the spores became distributed. With the aid of a Leitz-Wetzler counting apparatus the number of spores which had been deposited on the square centimetre of paper was determined, as an average of five trials, to be 44,450,000. On the average, then, each of the 26 tubes had produced 1,700,000 spores.

As a control to the above calculation I determined the number of spores deposited from a single tube of the fruit-body. It was quite easy to cut out a piece of paper bearing a heap of spores of the same size as before. This was then stirred up with 5 cc. of water. As a result of five readings with the counting apparatus the number of spores was found to be 1,770,000, which is unexpectedly near the figure indirectly obtained in the previous calculation. Since the whole fruit-body was some 250 sq. cm. in area the total number of spores produced by it would be about the magnitude of 11,112,500,000. The

fruit-body in question, however, was only one of a group of about ten upon the same tree. The number of spores produced by a single fungus from a single tree in the course of a year may, therefore, be some fifty times the population of the globe.

The spores fall in such vast numbers that it is not surprising that one may watch their fall with the naked eye. A fruit-body some ten inches across was grown on a log in the Experimental Greenhouse, where the air was very quiet. Under these conditions clouds of spores, resembling steam, or the finest white smoke, were observed falling continuously for thirteen days. The wreaths and curls of spores drifted slowly away from the fruit-bodies and became lost at a distance of about two yards. I could distinctly see wreaths of spores on a black background from a distance of thirty feet. The alternation of day and night appeared to have no effect on the spore-fall. Fruit-bodies kept in the dark liberated clouds of spores continuously for several days. When the log on which the large fruit-body was growing was taken from the dry atmosphere of the Experimental Greenhouse, and placed in the saturated atmosphere of the *Hymenophyllum* house the spores continued to fall without interruption. The amount of moisture in the air does not, therefore, appear to effect the spore-fall.

Germination of the spores takes place readily in a suitable medium. Experiments were made with hanging-drop cultures at the temperature of the laboratory, about 18° C. In each case the glass ring employed for making the culture cell was about half filled with the solution used for the hanging-drop.

The spores would not germinate at all in any of the following solutions: distilled water; tap water; grape-sugar, 20%, 2%, 0.2%; cane-sugar, 34%, 3.4%, 0.34%; maltose, 1%; Potassium phosphate, 1%, 0.1%, 0.01%; water containing 0.5% ether or 0.5% alcohol.

Decoctions were made from the wood of *Aesculus hippocastanum*, *Ulmus montana* and *Acer pseudoplatanus* by boiling chips in water for half an hour. The spores would not germinate in hanging-drops of these solutions. Upon repeating this series of experiments similar negative results were obtained with decoctions from the first two kinds of wood. In the case of *Acer* there was no germination during the first two days. On the third day about 1 % of the spores was seen to have germinated. In this culture, however, bacteria had developed in large numbers. The impression given me by this exceptional case was that the metabolism of the bacteria had given rise to some substance which to a slight extent had stimulated the spores to germinate. The germ tubes grew slowly for some days (Pl. VI, fig. 9).

Hanging-drops were then made with tap water in which chips of wood of the three above-mentioned trees were placed. The spores were mixed with the chips, and could be seen to be well placed among

the wood cells. In the cases of *Aesculus* and *Ulmus* no germination took place. With *Acer*, after two days, two spores, not in contact with the wood cells, out of some thousands put out short germ-tubes. No further germination occurred. It seems, therefore, that mere contact with wood cells does not provide the stimulus for germination.

Some branches of Sycamore and Horse Chestnut, about two inches across, were sawn off, and pieces of them, six inches long, were placed upright in a series of small damp-chambers, so that one end of each piece was in water. The upper ends were thickly strewn with fresh spores of the fungus and moistened with drops of water, by which means the spores were spread fairly evenly over the wound-surfaces. After about 48 hours, upon examination of surface-sections of the wood, a very few spores (about 50 out of many thousands) were found to have put out short germ-tubes. Infection of the wood by the tubes could not, however, be observed. Subsequently it was found that the number of spores undergoing germination had not increased, although in some cases, even at the end of 18 days, the spores on the wounds appeared to be turgid and living. A number of the spores, however, had collapsed, and were obviously dead. The mycelium of the fungus could not be found in the wood-cells. The almost total failure in germination, and the unsuccessful infection of the wood by such germ-tubes as were produced, seems to me to have been due to want of suitable conditions of nutrition on the wound-surfaces. Possibly in nature other organisms serve to prepare the wounds for infection by the fungus.

The length of time required under natural conditions for any of the big tree fungi to pass from the spore to the fruit-body stage is at present unknown. With the object of solving this problem I started some further experiments last July. In some private grounds at Birmingham six large and sound trees of the following species were chosen: Sycamore (*Acer pseudoplatanus*), Beech (*Fagus sylvatica*), Ash (*Fraxinus excelsior*), Elm (*Ulmus montana*), Lime (*Tilia europaea*), and Horse Chestnut (*Aesculus hippocastanum*). Six suitable wounds were made in each tree by sawing off large branches, etc., and the wound-surfaces were carefully strewn with millions of some freshly fallen spores. The surfaces were then moistened with drops of water. I have hopes that these experiments, made on a large scale upon living trees growing under natural conditions, may be more successful than those made in the laboratory, and result in successful infection. It is, of course, too early yet to state whether infection of the trees has taken place. If, however, fruit-bodies of the fungus should appear on any of the trees in the next few years, due record of the facts will be made.

It was found that germination would take place in various solu-

tions containing nitrogenous substances, namely, in malt-wort extract, with or without gelatine, in a meat-extract-peptone-sugar-gelatine solution, in peptone, asparagin, and to some extent in ordinary gelatine.

The malt-wort extract was made by grinding up one part of malt to five of water, mashing at 66° C, filtering, then boiling and refiltering. The clear solution was then slightly acid. Germination took place in it with great certainty, nearly all the spores putting out germ-tubes. At 18° C. the process began 16 to 20 hours after the spores had been placed in the hanging-drops.

Malt-wort extract solidified with 10% gelatine proved a suitable medium for making pure cultures. Its acidity is unfavourable to bacteria. A fresh fruit-body was placed upon sterilized brown paper. The spore heaps were thus obtained practically free from bacteria. From the spores plate and tube cultures were made (Pl. V, figs. 2-3) in the ordinary way. Growth was rather slow, the slanting gelatine in the tubes becoming covered with a felt of white mycelium in about six weeks. The mycelium was still developing at the end of six months. The gelatine gradually liquified.

The germination of spores in hanging-drops of malt-wort gelatine was carefully watched. The glass cells, an inch wide, the water covering their bases and the malt-wort-gelatine were thoroughly sterilized in the usual manner, and Freudenreicher flasks used in making the drops containing the spores. In this way pure cultures, free from moulds and bacteria, were obtained. The drops were 0.5 to 1 cm. across, and contained a very few well-scattered spores. Early stages of germination are illustrated in Pl. VI, fig. 10, *a*, *g*. After about twelve days the young plants had become about 2 mm. wide. In some of the plants growth in length then ceased, and the hyphae in the course of a few days became entirely divided up into what may be called oidial cells (Fig. 10, *h*). The oidial cells were formed by the contraction of the protoplasm in each hypha into short cylindrical or oval masses [1] (Fig. 10, *i*, *j*, *k*). Each mass of protoplasm after contraction formed two thin end walls. Falck (*loc. cit.*) has shown that the formation of oidia represents a definite stage in the life-history of a number of Hymenomycetes, and that fruit-bodies can be raised from a single oidium. The occurrence of oidial cells in *Polyporus squamosus*, therefore, is not surprising. The oidial cells appeared to have no tendency to germinate in the original drops. Some of them were removed to new drops of malt-wort-gelatine. Under these circumstances they germinated (Fig. 10, *l*, *m*, *n*) within 48 hours, and at the end of a fortnight the young plants had become much branched and appeared to be vigorous.

[1] Similar incomplete breaking up of the mycelium is figured by Brefeld for *Crucibulum vulgare*. Untersuchungen, Heft III, Taf. viii, fig. 4.

Whether the oidial cell stage is indispensable in the life-history of the fungus appears to me to be doubtful. As already mentioned, pure cultures from one or more spores continued to grow in tubes for several months. Again, some of the hyphae in a few of the hanging-drop cultures appeared to continue growing in length indefinitely, and were not observed to finally break up into oidial cells.

Germination also succeeded well in a solution made with tap water, and consisting of meat-extract 0.5%, peptone 0.5%, grape-sugar 3%, and gelatine 10%. The solution was made distinctly alkaline with sodium carbonate. The mycelium grew in this mixture rather more vigorously than in the malt-wort extract. Branching was more frequent. Development from a spore in one week is shown in Pl. VI, fig. 11.

In 0.5% peptone a certain number of spores germinated. Development with branching took place as illustrated in Pl. VI, fig. 15.

A few spores also germinated in an unneutralized solution of 7% gelatine. This substance is by no means pure, so that the result is not surprising.

In 0.5% asparagin about 10% or less of the spores germinated. The germ-tubes grew very rapidly, and were remarkable in that they never branched. The protoplasm crept along the germ-tube as growth proceeded, so that it was all contained within a small stretch near the growing point (Pl. VI, fig. 16; Pl. VII, fig. 17). The contrast with the much-branched germ-tubes in the meat-extract-peptone-sugar solution is very striking. We have here a good example of how chemical conditions influence the manner of growth of a fungus.

In the solutions of potassium phosphate 1%, 0.1%, and 0.01%, as already mentioned, no germination whatever took place. The spores, however, underwent cell division as a result of the stimulus given by the phosphate. One, two, or three cross-walls were formed. Some spores remained unicellular (Pl. VII, fig. 18). In tap-water not a single spore germinated. The contents of the spores underwent, however, in many cases a curious contraction (Pl. VII, fig. 19). The contracted protoplasm, where not in contact with the old spore wall, surrounded itself by a new wall, reminding one of the formation of a new wall around the contracted contents of such algal cells as those of *Cladophora*.[1] At the end of 14 days the spores were removed from the water and placed in a drop of malt-wort extract. After 28 hours many of the spores, including such in which protoplasmic contraction had taken place, were found to have germinated (Pl. VII, figs. 20 and 21). This experiment shows that spores can lie dormant in water for many days and still retain their powers of germination. This fact may be of

[1] See Pfeffer's, Physiology of Plants, p. 52.

some biological importance. Doubtless the spores of *Polyporus squamosus* are often blown into damp situations, such as puddles, wet bark, etc. Here there would be no stimulus to germination. Upon evaporation of the water the spores might be again carried into the air or be otherwise transported, with the chance of eventually reaching a suitable place for germination.

When spores are allowed to dry they undergo a marked change, large fat drops appearing in them (Pl. VII, fig. 22). Spores were exposed upon paper to the dry air of the laboratory, and then after 7 and 14 days respectively placed in a drop of malt-wort extract. Germination of a large proportion of the spores took place, including such as possessed large flat drops (Pl. VII, figs. 23, 24). Many of the spores, however, had collapsed and were dead, doubtless owing to their vitality having been unfavourably affected by desiccation. Under natural conditions the spores of *Polyporus squamosus* are, doubtless, often blown hither and thither by varying winds for days and weeks. It is, therefore, of interest to know that at the end of this time, if a favourable situation has been found, germination may still take place.

If the orientation of the spore is suitable it is easy to determine the end which was united to the sterigma. This enabled me to make sure that, so far as germination is concerned, the spores do not possess any polarity. Germination may take place indifferently at either end, or at any point on the side of a spore (Pl. VI, figs. 12, 13). The number of germ-tubes put out by a spore is variable, sometimes as many as four being produced (Pl. VI, fig. 14).

A noteworthy phenomenon during germination is the creeping of the protoplasm along the germ-tubes. In the malt-wort extract, when many spores germinated together, the spore was thereby frequently emptied of its contents. In the case of asparagin the protoplasm crept a distance of over 0.5 mm. in about 48 hours after germination had begun (Pl. VI, fig. 16). When protoplasm is creeping out of a spore or along a germ-tube it forms cross-walls at intervals upon its free surface (Pl. VI, figs, 12, 13, 14). When such a wall has been formed the protoplasm gradually withdraws from it, creeps on further along the growing germ-tube, and then forms a new cross-wall. In asparagin, in one instance (Fig. 16), fourteen such walls were found in succession. By carefully observing a single case (Pl. VI, fig. 12) it was found that growth of the end of a germ-tube took place even while the protoplasm was creeping along and leaving a wall. The tugidity of the cell under such circumstances must be very slight.

It has already been mentioned that in solutions of potassium phosphate the spores, without germination, underwent cell division (Pl. II, fig. 18). In these cases there was, of course, protoplasm on both sides of a wall during its formation. After germination in malt-wort extract

the spores are often seen to have apparently similar cross-walls in them (Pl. VI, figs. 13, 14). Here, however, the walls are formed not before germination but afterwards, in succession, at the free surface of the protoplasm as this creeps out of the spore along the germ-tubes.

## Vegetative Growth and Penetration of Cell-walls.

The hyphae in the wood of *Acer* make their easiest and most rapid advance along the wood vessels. In these they attain their greatest diameter and often produce clamp connections (Pl. VII, fig. 25, *c* and *k*; figs. 27, 28). From the structure of the cells of the wood it is obvious that the path of least resistance for the mycelium is longitudinal, for in that direction fewer cell-walls have to be bored through than in any other. Thus when the mycelium has reached the centre of a tree-trunk, *via* some thick branch, it often spreads many feet upwards and downwards in the middle during the time required to travel a few inches in the radial direction.

The hyphae penetrate into all the wood-cells. In making their way through the walls from one cell to another the pits are not specially used. Thus in Fig. 29, where a piece of a wall between two vessels is drawn, it will be seen that the holes made by the hyphae bear no relation to the position of the bordered pits.

In passing through a wall a hypha, as is the case with so many other fungi, makes a hole much smaller in diameter than itself (Pl. VIII, fig. 26, *j*). After penetration growth is continued with the same diameter as before. The holes are afterwards much enlarged by enzymes (Pl. VIII, figs. 30, 31).

While reflecting upon the causes of the penetration of hyphae from cell to cell the following consideration occurred to me. Notwithstanding the fact that the mycelium of a fungus is a very much branched structure, it must be looked upon as a co-ordinated whole in the same way as a much branched tree. Upon germination of a spore the plant branches in such a way that the hyphae radiate from the centre and avoid each other as much as possible (Pl. VI, fig. 11). When the mycelium is in wood it attempts to send out hyphae in all directions. The hyphae thus come in contact with cell-walls. Doubtless, owing to the excretion of the enzymes[1] at the growing points of the hyphae, and possibly also in response to a contact stimulus,[2] the walls are quickly penetrated. The spreading of the mycelium from cell to cell through a piece of wood is thus explained, not as a result of chemotropic attraction by external chemical substances in the wood-

[1] Cf. Marshall Ward, Ann. of Bot., 1888, pp. 342-343.

[2] Cf. Miyoshi, Jahrbücher f. wiss. Bot., 1895, vol. 28, pp. 279, 280.

cells, but as a result of a method of growth inhering in the fungus itself.

It seems probable, however, that the penetration of a hypha through a cell-wall is not infrequently a chemotropic phenomenon. The best evidence of this in the case of *Polyporus squamosus* is to be obtained by a study of fig. 32. The longitudinal view is as exact a drawing as I could make. The transverse part at the top is schematic, and added to show the distribution of the cells. It will be noticed that between the vessels there are several parallel series of holes. These were made by fungus hyphae, which had disappeared during the cutting of the section or by the action of enzymes. The explanation of the parallel growth of the hyphae appears to be that in the vessel $x$ the food material was diminished or used up by the mycelium. This entailed a diffusion of food material from the vessel $y$ to $x$. The chemotropic stimulus thus arising caused the hyphae to penetrate through the wood fibres from $x$ to $y$ along parallel lines.

## Structure of the Wood of Acer.

Before dealing with the destruction of the wood of Acer, an account of its structure in a healthy state must first be given.

In a cross-section of a piece of wood of *Acer pseudoplatanus* one sees that the vessels are uniformly distributed throughout a year's growth, and are all approximately of equal size. They are small, being only just recognizable with the naked eye. They often occur in pairs together, although usually separate from one another. The medullary rays are narrow and numerous, not more than 0.5 mm. deep, and rarely exceeding 0.1 mm. wide. The last-formed autumn wood, three or four layers of cells deep, appears to the naked eye as a very distinct thin line. The general character of the wood may be gathered from figs. 25, 26, 32, and 33.

The minute anatomy of the wood-cells may be made out from fig. 25. The vessels are spirally thickened. Between two adjacent vessels the wall is always covered with bordered pits (Figs. 26, *i*, and 29). Between the scattered vessels the elements, with the exception of the medullary rays, consist of wood fibres and parenchyma. The fibres are of two kinds, dead and living. The former, which form the majority, contain water and air-bubbles in the autumn. The latter form the late autumn wood, and in October contain much starch. The walls of the fibres have rows of simple slit-like pits. In the autumn wood these are almost exclusively on the radial side (Figs. 26, *d*, *d*, 30, 31), reminding one of the position of the bordered pits upon the walls of the tracheides of the Coniferae. Some of the fibres, especially among those of the autumn wood, have curious spiral corrugations (Pl. VII, figs. 25, *f*, $f^1$, and *j*). All the fibres have comparatively thin

walls. The wood parenchyma is to be found around the vessels and connecting these with the medullary rays. All the living cells contain starch during the autumn and winter (Fig. 25, *b. d. f, x*).

The cell-walls are all more or less lignified. The walls of the vessels, of the layer of cells surrounding them, of the autumn wood and of the medullary rays are all highly lignified. Less lignified are the groups of fibres between the vessels.

There are no tyloses in the vessels. None were to be found in any part of a tree-trunk with 220 rings of growth. The vessels, however, become plugged up at intervals with yellowish masses of an apparently gummaceous substance, the origin of which is not clear to me (Fig. 25, *r*; fig. 26, *i* and *m*; fig. 32, *t, t*).

There is no heart-wood. The colour of the wood is nearly white, with a yellow tinge. On exposure to the air the medullary rays turn brownish.

## Destruction of the Wood of Acer.

Macroscopically a piece of wood, which has been rotted by *Polyporus squamosus*, possesses a characteristic appearance. The wood becomes much whiter, having undergone a White Rot. The mycelium forms locally small white irregular strands, which interlace chiefly in the longitudinal, radial and tangential divisions of the wood. The size and course of the strands can best be gathered from the photographs (Pl. V, figs. 4, 5). The wood-cells replaced are chiefly the less lignified fibres between the vessels (Pl. VIII, 33, *d d, e, f*). The radial strands are parallel to the medullary rays, and sometimes run through several years' rings, breaking down the autumn wood-cells (Fig. 33, *d, d*). The longitudinal strands (Fig. 33, *e*) are parallel to the vessels.

The mycelial strands of *P. squamosus* have a similar distribution in *Acer pseudoplatanus*, *A. platanoides*, *A. negundo* and *Ulmus montana*, so that it must be regarded as characteristic of the fungus, and as a means of recognizing it when fruit-bodies are not present.

Owing to the mycelial strings running in the three directions mentioned, the wood tends to become split up into irregular cubes. As a consequence it has a more or less cuboidal fracture (Pl. V, fig. 6).

During the growth of the mycelium the wood becomes very light in weight and much softer, at length possessing the consistency of cheese, so that one may push a knife-blade into it.

The general appearance of a cross-section of a piece of very rotten wood is shown in the low-power drawing (Fig. 33). The most persistent groups of elements are the more highly lignified, namely, the autumn wood, the vessels with a layer of cells surrounding them, and the medullary rays. The cells entirely removed are the fibres between the vessels or produced in spring. These, as already pointed out, are

the less lignified elements. In the left-hand half of the figure 33, *d*, *d*, is seen a mycelial strand running radially. Although in the direction of the medullary rays it is not actually in one of them, but replaces a considerable number of fibres. At *e* is a longitudinal mycelial strand in transverse section.

The disappearance of the less lignified fibres is shown in fig. 26 between *k* and *m*. It will there be seen that the secondary thickening of the cell-walls disappear first, and very soon afterwards the middle lamellae. The latter are never dissolved first, so that there is never any separation of the cells from one another in the manner one finds as a result of the action of *Trametes radiciperda* on the wood of *Picea*, or *Stereum frustulosum* on that of the Oak. The lignification of the cell-walls of these elements is not pronounced, as may be determined with the phloroglucin, the analine sulphate or the chlorzinc-iodine tests. As the cell-walls are disappearing they take a violet-blue colour with chlorzinc-iodine, which indicates that they become delignified.

The more lignified elements (the autumn wood, the medullary rays, and vessels with a layer of cells surrounding them) are acted upon in a different manner to the less lignified. They never become delignified, so as to take on the cellulose reaction with chlorzinc-iodine, even in the most highly rotten wood. Owing to the great enlargement of their pits, or the gradual reduction in the thickness of their walls, they become slowly reduced, but can still be found in the most rotten wood which has probably reached its extreme limit of exhaustion by the fungus (Fig. 26, fig. 34, *e*, *e*). After treatment with Schulze's macerating solution they turn blue with chlorzinc-iodine, which proves that they still contain cellulose.

The enlargement of the pits in the walls of the autumn fibres is represented in figs. 30 and 31. Figure 31 gives a view of a radial section, and fig. 30 of a tangential section. With the enlargement of the pits their position—on the radial walls only—becomes very noticeable. The pits become oval in face view, and somewhat hour-glass shaped in section. The enlargement usually goes on without any diminution in the thickness of the walls. Possibly the enzymes dissolving the membranes act best in the directions parallel to the wall-surfaces. The enlargement of the pits of the medullary ray cells is best seen in fig. 26 from *c* to $c^1$, and in fig. 25 from *x* to *z*. The gradual thinning of the walls of these cells is also shown in the same parts of the figures.

The holes made by the hyphae in walls also become enlarged, doubtless by enzymes diffusing through the cells and produced by the fungus (Figs. 30, 31). To what an extent the enlargement of the pits and holes in cell-walls can lead to the destruction of a cell is shown in fig. 35 (Pl. VIII), which represents a fibre isolated by means of Schulze's macerating mixture from highly rotten wood.

The cell-contents are gradually dissolved away, leaving the cells quite empty. In the healthy wood the protoplasm forms a lining layer in the medullary ray, autumn wood, and wood parenchymatous cells. When acted upon by the fungus it turns reddish brown, and appears to develop a resinous consistency. When isolated by means of Schulze's macerating mixture the fibres have the appearance shown in figs. 36-43. The change in the colour of the protoplasm gives rise to a red or brownish-red zone in the wood. The protoplasm breaks up into pieces and disappears. This is well seen in the medullary rays, as indicated in fig. 25 from *x* to *y*, also fig. 26, *c* to *g*.

Starch was not found present in great quantity in any of the wood-cells of the infected wood. Such that is present disappears (Fig. 25, *x-y*), doubtless owing to an amylolytic enzyme excreted by the fungus. I was not able to trace any erosion in the disappearing grains.

All the older vessels, as already remarked, are blocked up at intervals by an apparently gummaceous substance. These tracheal plugs are still present in the most highly-decayed wood (Figs. 26 $m^1$, 25, *n*), and are apparently not acted upon by the enzymes of the fungus.

The hyphae of the fungus are largest in vessels just entered (Fig. 25, *c*). In the very rottenest wood these broad hyphae, which may be 7-11 $\mu$ thick, seem to have disappeared. In their stead one finds a great number of very fine hyphae (Fig. 25, *t*). Often these are one-fiftieth or less the diameter of the broad hyphae (*cf.* figs. 28 and 44), so that a high magnification is required to see them. Doubtless the mycelium here is in a condition of starvation. The walls of the broad hyphae are comparatively thin. Many of the narrower hyphae are comparatively thick-walled, so that their lumina are much reduced (Pl. IX, fig. 45, *a*).

Conidia were sought for upon the mycelium in the wood. In general none could be found. In the wood from one tree, however, curious swellings were seen upon some of the hyphae (Figs. 45, 46). The swellings were oval or elongated, and contained fat. They were found both in the vessels and where the mycelium had replaced groups of the less lignified fibres. While some of them do certainly suggest reproductive bodies, it is quite possible that they are only involution forms of the mycelium. Perhaps, however, they most resemble the oidial cells already described (*cf.* Pl. VI, fig. 10, *h* and *k*).

An attempt has been made in the figures 25 and 26 to summarise the anatomical changes brought about in the sound wood by the fungus mycelium. At S in each case the wood is represented as sound, while at R it is in the last stages of decay. The fungus is supposed to be making its way from R to S. The chief points to be noticed are: (i.) The disappearance of the less lignified fibres and the general persistence of the other elements which are more highly lignified; (ii.) the

enlargement of the pits; (iii.) the disappearance of the starch and protoplasm; (iv.) the variation in the mycelium; (v.) the persistence of the tracheal plugs, and (vi.) the supposed chemotropic phenomenon. Details of these figures are given in the description of the plates.

The black layer of mycelial tissue, which is frequently to be found in or upon wood rotted by *Polyporus squamosus* and other Polyporei, will be described in a later paper.

## Chemical Changes in the Wood.

The following analyses were kindly made for me by my friend Dr. R. H. Pickard in order to throw some light upon the manner in which the chemical elements in the wood become used up relatively to one another by the fungi concerned. The percentage composition is given in each case. The left half of the table enables us to trace the ash constituents, while the right half gives an account of the organic matter only, calculated free from ash.

*Polyporus squamosus.*

| Wood of *Acer pseudoplatanus.* | Organic matter and ash | | | | | Organic matter only | | | |
|---|---|---|---|---|---|---|---|---|---|
| | by analysis. | | | | by diff. | by calculation. | | | |
| | C | H | N | Ash | O | C | H | O | N |
| Sound .. .. .. .. | 43·96 | 6·85 | 1·15 | 0·24 | 47·80 | 44·08 | 6·85 | 47·90 | 1·16 |
| Medium decayed .. .. | 40·74 | 6·07 | 1·54 | 3·52 | 48·13 | 42·25 | 6·29 | 49·89 | 1·59 |
| Highly decayed .. .. | 44·19 | 6·74 | 0·46 | 3·45 | 45·16 | 45·77 | 6·98 | 46·78 | 0·47 |
| Wood of *Ulmus montana.* | | | | | | | | | |
| Sound .. .. .. .. | 43·83 | 6·66 | 1·62 | 1·49 | 46·40 | 44·49 | 6·76 | 47·12 | 1·64 |
| Highly decayed .. .. | 44·90 | 6·82 | 1·48 | 2·83 | 43·97 | 46·21 | 7·02 | 45·26 | 1·52 |
| Fruit-body .. .. .. | 37·59 | 6·65 | 1·83 | 3·05 | 50·88 | 38·77 | 6·86 | 52·48 | 1·88 |

In his "Zersetzungserscheinungen" Hartig has given a number of analyses of sound and decayed wood of Oak and Coniferae, but not of the fungi concerned in its destruction. In the present instance an analysis of the fruit-body has been added. Nevertheless for the exact determination of the chemical changes brought about by the fungi in the wood the data are still incomplete. We still require to know the gross amount of wood substance removed from the trees, and the gross amount of fruit-bodies formed. If it were possible to separate the mycelium from the wood substance in the decayed wood, we should need to analyse them separately. We could then exactly determine what becomes of each chemical element: we could estimate

the precise amount of the carbohydrates used by the fungus in respiration, and we could decide whether nitrogen escapes as a gas, or is simply used by the hyphae in the formation of proteids. Both the partly decayed and the highly decayed wood used for the analyses here given contained mycelium. Notwithstanding the incompleteness of the data the figures in the table do appear to allow us to draw certain conclusions which must now be discussed.

A comparison of the figures shows that the fruit-bodies of *Polyporus squamosus* and the sound wood both of *Ulmus montana* and *Acer pseudoplatanus* contain about equal percentages of hydrogen. The fruit-body, however, is markedly poorer in carbon and richer in oxygen and nitrogen. On the other hand the highly-decayed wood of both species is richer in carbon and poorer in oxygen and nitrogen than the sound wood. The fungus, therefore, appears to abstract from the wood and store in its fruit-bodies relatively less carbon and more nitrogen and oxygen.

The highly-decayed wood had a specific gravity of one-half, or less than that, of the sound wood. The accumulation of carbon in the highly-decayed wood of both species is less than 2 per cent. It seems, therefore, probable that the carbohydrates, abstracted from the wood by the fungus, and used for respiration, are in the end used up in such manner that the oxygen and hydrogen split off, combine in the proportions to form water, and most, but not all, of the carbon is united with oxygen from the air to form carbon dioxide.

Ash constituents accumulate in the rotting wood, and are also present in larger proportions in the fruit-bodies than the sound wood. Since the elements in the ash cannot be used in respiration and do not escape as gases, whereas the carbohydrates are so used, an accumulation of them as compared with carbon, hydrogen and oxygen is easily understood.

The carbonising of the wood of *Acer pseudoplatanus* and *Ulmus montana* by *Polyporus squamosus* is only slight in comparison with that brought about by *Polyporus sulphureus*. While in the case investigated by me the increase of carbon does not exceed 2 % the increase in the wood of the Oak under the action of *Polyporus sulphureus* [1] is more than 6 %.

## Enzymes.

From the anatomical study of wood undergoing decay through the agency of *Polyporus squamosus* evidence was obtained that various enzymes are excreted by the fungus mycelium. Thus, the disappearance of starch, proteids, and cellulose suggests that the fungus pro-

[1] R. Hartig, Zersetzungserscheinungen des Holzes, p. 112.

duces amylolytic, proteolytic and cyteolytic enzymes. In order to supplement the anatomical observations an endeavour was made to prove the presence of enzymes by direct chemical investigations. For this purpose fresh young fruit-bodies were obtained as required from the Botanical Gardens, Birmingham, and their juice extracted and tested.

In order not to make this paper inordinately long I have given the details of these experiments in another paper,[1] and must content myself here with a general statement of the results. My work appears to show that the following enzymes occur in the fruit-bodies of *P. squamosus*: laccase, tyrosinase, amylase, emulsin, protease, lipase, rennetase, and "coagulase," whereas negative results were obtained in the tests for pectase, maltase, invertase, trehalase, and cytase. How-

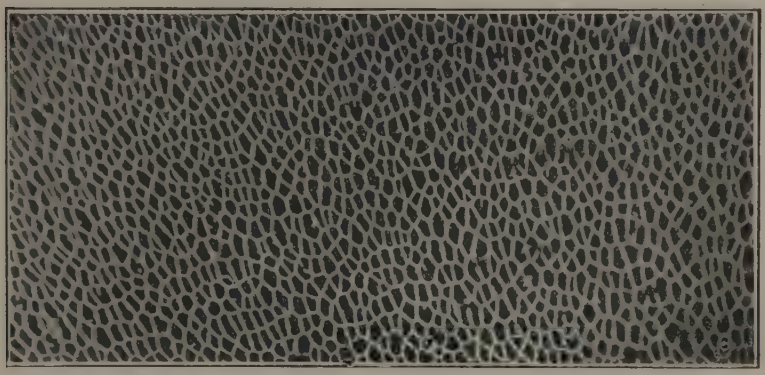


Fig. D.—View of part of the underside of a mature fruit-body of *Polyporus squamosus*, which was 2 ft. 2 in. across. The openings of the hymenial tubes are polygonal. Nat. size.

ever, a study of the destruction of wood by the fungus affords evidence that the mycelium produces cytase and possibly hadromase. Altogether, then, the juice of the fungus appears to be able to bring about at least nine or ten different enzyme phenomena. There seems little doubt that the destruction of wood by *Polyporus squamosus* is chiefly due to the enzymes it is capable of producing.

## Fruit-Bodies.

*Polyporus squamosus*, which was described by Saccardo[2] and Fries,[3] and amongst modern authors by Massee (in his "British Fungus

[1] Ann. of Bot., 1906, vol. xx, pp. 49-59.
[2] Saccardo, Sylloge Fungorum.
[3] Fries, Hymenomycetes Europaei, 1874.

Flora"), has frequently been figured. Greville[1] and Harzer[2] give coloured plates. In the "Pflanzenfamilien" there is a drawing by Hennings.[3] Tuboeuf,[4] in his "Diseases of Plants," reproduces a photograph of a group of fruit-bodies upon an Elm tree. My own photographs show the upper and under sides of a nearly full-grown fruit-body (Figs. B and C) and some fruit-bodies growing out from a wound-surface of a Wych-Elm, where a large branch had been broken off (Fig. A). Photographs of the openings of the hymenial tubes and part of a cross-section through a mature specimen are given in Figs. D and E respectively.

Berkeley,[5] in his description, says, "Pileus. . . . If a portion of the hymenium be torn off a new stratum of pores is rapidly developed." This fact is confirmed by my own observations. I found a

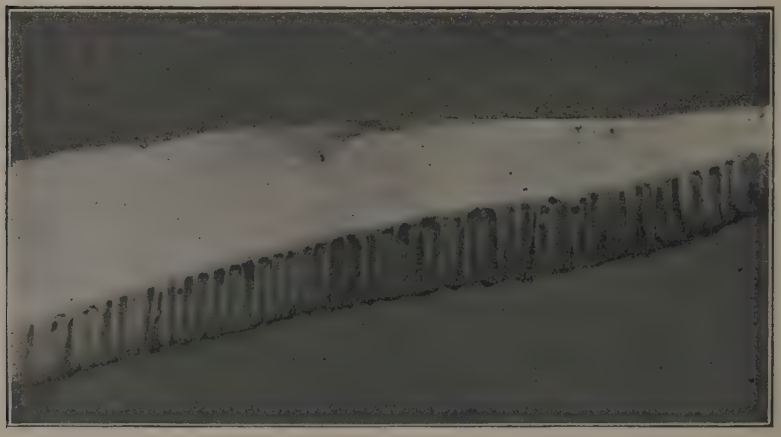


Fig. E.—View of part of a transverse section through the middle of a mature fruit-body of *Polyporus squamosus*. The hymenial tubes are directed downwards. Nat. size.

fruit-body which had accidentally been torn, so that a piece of the hymenium hung down as a flap. A new layer of hymenial tubes had developed on the pileus where the injury had taken place. When the hymenial tubes were stripped off young fruit-bodies grown in the Experimental Greenhouse, new ones began to appear in the course of two days.

Berkeley also says, "Pileus. . . . In vaults and hollow trees it

[1] Greville, Scot. Crypt. Flora, vol. iv.
[2] Harzer, Die essbaren, giftigen und verdächtigen Pilze, Dresden, 1842.
[3] Engler u. Prantl. Die. nat. Pflanzenfamilien, 1900, I. Theil, Abtheil. 1, p. 169.
[4] Tuboeuf, Diseases of Plants, Fig. 275.
[5] Berkeley, quoted from Massee, British Fungus Flora, vol. i, p. 234.

sometimes assumes the form of *Clavaria*, but in this case seldom produces a pileus." The usual length of the stipe of a fruit-body grown in the light and not crowded by other fruit-bodies is about 5 cm. Sadebeck [1] watched the development of a group of eleven fruit-bodies upon some Elm-wood placed in a dark cellar, and observed that the stipes, although of the usual thickness, attained a length of 20 cm. without showing any signs of pilei. The stipes, some of which were forked at the ends, he describes as looking like deer-horns. While development was still proceeding he exposed four of the fruit-bodies to direct sunlight, while the other seven were kept in darkness. Two of the former, in the course of two days, began to show signs of pilei, which were completed in six days. These fertile fruit-bodies persisted for eight months. All the other fruit-bodies failed to produce any pilei, and soon withered. This interesting experiment shows that the length of the stipe and the development of the pileus is determined by light conditions. By a further experiment Sadebeck showed that the amount of moisture present in the atmosphere does not appreciably affect the form of the fruit-bodies. During the summer of 1905 I was able to confirm these observations. Fruit-bodies were grown upon a log in a dark room. They grew into branched deer-horn-like structures Pl. IX, fig. 47, *j*), a foot in length, without any formation of pilei. The latter, however, were formed when the fruit-bodies were exposed to the light.

Doubtless the developmental reaction to light, just described, is of biological advantage to the fungus species. Only those fruit-bodies which are exposed to the light will be in open positions, so that their spores will have a chance of being dispersed by the wind. Hence it is advantageous that the fruit-bodies should not develop pilei in the dark, but should do so immediately that, so to speak, they have groped their way to the light. A similar case is provided by another wood-destroying fungus, namely, *Lentinus lepideus*.[2]

The direction of the stipe is variable. It grows outwards from the wood substratum, as is shown where fruit-bodies develop in the dark. In two cases I have found it vertical when growing on horizontal surfaces, although when produced on the side of a tree it is usually slightly inclined upwards. By placing young fruit-bodies with very rudimentary pilei in the dark, I have been able to convince myself by watching the subsequent development that the stipe is negatively geotropic until it has brought the young pileus into a horizontal position (*cf.* Pl. IX, fig. 47, *a-h*).

Under natural conditions the pileus is always nearly horizontal,

[1] Sadebeck, Bot. Centralb., 1886, Bd. xxv, p. 226.

[2] Buller, Ann. of Bot., 1905, vol. xix, pp. 427-438.

whilst the hymenial tubes are vertical.[1] By a simple experiment I have been able to prove that the pileus is dia-geotropic, and the tubes positively geotropic. Some young fruit-bodies, between three and four inches across, and just beginning to develop hymenial tubes, were found growing on a log. The log was removed to a dark room, and placed in such a position that the pilei projected upwards vertically. Under these conditions the edges of the pileus curved toward the hymenial surface. The upper edge on becoming horizontal, continued to grow horizontally for a distance of three inches, thus giving a dia-geotropic reaction. The vertical edges of the pileus soon ceased to grow. It thus became evident that the stimulus of gravity strongly favoured the growth of the horizontally placed portions of the pileus. Hymenial tubes, producing clouds of spores, were developed in the dark on the under-side of inclined and horizontal parts of the pileus, and in every case they grew vertically downwards, thus reacting in a positively geotropic manner. On the vertical parts of the pileus no tubes were developed. It appears, then, that the stimulus of gravity decides not only the direction of growth of the pileus and hymenial tubes, but also which part of the pileus shall develope, and where the tubes are to be formed. In other words gravity acts upon the fruit-bodies both as an orienting and as a morphogenic stimulus.

The geotropic reactions, which are shared by many other Polyporei, enable the hymenial tubes to be developed in such a position that with a given diameter the maximum number of them may be produced in such a position as to be quite protected from rain, and that the spores may fall out in the easiest possible manner.[2]

Berkeley[3] thus describes the development of the fruit-bodies: "From a subglobose or turgid scaly black knob arise one or more stems, which are at first slightly compressed, flat, and hollowed out above where they are furfuraceous; gradually the depressed surface expands, but more rapidly in the direction of the light, and the hymenium is formed beneath the small scales of the upper part of the stem, consisting, when feebly developed, of large angular spores, becoming mere reticulations towards the base." My own observations confirm those of Berkeley. Successive stages in the development of a single fruit-body from a knob are illustrated in fig. 47 (Pl. IX), *a-h*, whilst *i* represents an early stage in the development of a group of three fruit-

[1] Cf. Sachs, On the Physiology of Plants, 1887, p. 700.

[2] It has been suggested by Massee (Ann. of Bot., vol. iv, p. 2) that the hymenial surfaces of Basidiomycetous fruit-bodies are on the under side for the purpose of protecting the spores from light. Until experimental evidence is forthcoming that the spores need such protection one may doubt whether the suggestion is a good one. The spores of the Clavarieae and of many Ascomycetes are freely exposed to sun-light under natural conditions.

[3] Berkeley, Quoted from Massee, British Fungus Flora, vol. i, p. 234.

bodies from a knob. The size and shape and distribution of the hymenial tubes in an average full-grown fruit-body may best be obtained from figs. D, E, and 48-50. The depth of the tubes varies considerably in different specimens. Though often shorter, they may attain a length of a centimetre.

The hymenial tubes begin to produce basidia and spores at the beginning of their development. The lengthening of a tube is brought about by the down-growth of the hyphae of the walls at the open end. The older part of a tube is already complete and bearing spores while elongation is still proceeding.

A portion of the hymenium is shown in fig. 51 (Pl. IX). Each basidium bears four sterigmata and spores. There are no cystidia.

Details with regard to the number of spores and of their fall as seen macroscopically, and also a statement as to the enzymes of the fruit-bodies have been given in earlier sections of the paper.

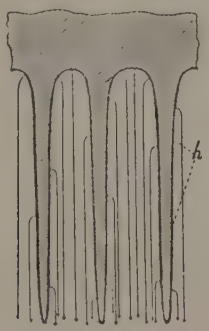



Fig. F.—Diagrammatical vertical section illustrating the course taken by spores in falling down two hymenial tubes of *Polyporus squamosus*. Each spore is projected horizontally from the hymenium *h*, but quickly takes a vertical course downwards in consequence of the attraction of gravitation. × about 4.

The hymenium covers the walls of the hymenial tubes, so that it is disposed in vertical planes. In order to observe how the spores manage to find their way out of the fruit-bodies, a transverse section, 1-2 mm. high, was cut through the living tubes, placed on a glass slide and looked down upon from above with the low power of the microscope. Immediately the remarkable fact was observed that *the spores were being shot outwards from the hymenium into the tubes.* With the high power, after considerable patience, it was found that the four spores of a basidium are not shot off together, but one by one. In one case it was observed that three spores left a basidium within one minute.

The spores, then, do not fall passively from the sterigmata, but are projected horizontally from these with a considerable velocity. This horizontal velocity carries the spores 0.1-0.2 mm. away from the hymenium before it is destroyed by the resistence of the air. After the horizontal velocity has thus been reduced to nothing the spores fall vertically downwards in the still air contained in the hymenial tubes. This could be observed by using a horizontally-placed microscope, and viewing therewith suitably-made sections of living tubes placed in a closed glass chamber. The spores under these conditions continued to fall vertically downwards. Each spore fell with one end first, the long axis being vertical. On leaving the tubes it was found that the spores did not fall more than 3 mm. per second. They can, therefore, be readily scattered in nature by the lightest breezes. A diagram, which shows the paths of a number of spores in falling within the hymenial tubes, is given in Figure F.

The projection of the spores into the hymenial tubes is a highly important process in their discharge. The spores are very adhesive. When they fall on to paper, glass, wood, etc., they immediately stick to these substances, and cannot be separated from them by the most vigorous shaking. The basidia are disposed one above the other in the hymenial tubes like bricks in a wall. If the spores merely fell off the sterigmata passively, they would fall on one another or on to the basidia or paraphyses, and would immediately stick there. The spores are projected horizontally, so as to prevent them touching anv part of the hymenium in their fall. The tenacity with which spores cling to one another is illustrated by the fact that from a spore deposit on paper one can scrape up with a knife spore-ribbons two or three mm. long.

A study of the liberation of the spores, therefore, makes clear the importance of the hymenial tubes being negatively geotropic. If the walls of the tubes did not look directly downwards the spores could not escape. The massiveness of the flesh of a fruit-body can also be explained in connection with the discharge of spores. It brings with it rigidity, and thus secures that hail, rain, the alighting of birds and other mechanical accidents shall not displace the fruit-body as a whole and place the tubes in an oblique instead of a vertical position. If a tube became only very slightly oblique, more than half its spores would never emerge from it.

Extended observation has taught me that the violent projection of spores from the sterigmata is not peculiar to *Polyporus squamosus*, but occurs generally in the *Polyporei*, the *Agaricini*, the *Thelephoreae*, and the *Tremellineae*. I hope shortly to give an account of my investigation into this matter.

In conclusion, it may be added that an attempt has been made to

procure the development of a fruit-body in a pure culture. Spores were allowed to germinate in a hanging-drop of malt extract. A young plant was then transferred to a two-litre flask, in which was contained a litre of sterilized malt-wort extract, solidified with 10% gelatine. During the last nine months the mycelium has formed a dense felt about one-third of an inch thick and more than six inches in diameter. So far, however, no signs of fruit-bodies have made their appearance.

*Winnipeg*, May 4th, 1906.

## EXPLANATIONS OF PLATES V—IX.

Illustrating Professor Buller's paper on "*Polyporus squamosus*, Huds."

### Plate V.

Fig. 1.—White spores of *Polyporus squamosus* which have fallen in heaps from the hymenial tubes of a fruit-body on to a glass slide. × 1.

Fig. 2.—Plate culture from spores. Medium made with malt-wort extract and 10 per cent. gelatine.

Fig. 3.—Tube culture from spores with same medium as before.

Fig. 4.—Wood of *Acer pseudoplatanus* much rotted by *Polyporus squamosus*, as seen in tangential section. The wood was wetted before the photograph was taken. The mycelial strands are white. × 1.

Fig. 5.—Radial longitudinal section of same. × 1.

Fig. 6.—Piece of similar wood, showing the more or less cuboidal fracture. × 1.

Fig. 7.—Section from trunk of *Acer pseudoplatanus* where a branch is given off, to show how *Polyporus squamosus* makes its way into the centre of a tree. The mycelial strands can be traced down the branch to the centre of the trunk, and then upwards to *s*. The fungus was found to have penetrated downwards in the middle of the trunk for about two metres. The wood in the regions *a* and *c* is quite sound and free from hyphae. × ½.

### Plate VI.

Fig. 8.—Fresh spores seen in water. Each contains a vacuole. × 550.

Fig. 9.—Some germ-tubes produced in a decoction of Sycamore wood during eleven days. There is no branching. × 550.

Fig 10.—*a-g*, successive stages in the germination of a spore in a hanging drop of malt-wort extract. × 550. *a*, the fresh spore; *b*, the spore after 14.5 hours; *c*, same after 20 hours; *d*, after 21 hours; *e*, after 23 hours; *f*, after 25 hours; *g*, after 27 hours.—*h*, mycelium produced from a

single spore in a hanging drop of malt-wort extract gelatine after 16 days; *x*, diagrammatic representation of the main mass of the plant. The latter was almost spherical. The hyphae, of which only a few in the plane of the paper are shown, had already formed oidial cells. × 100.—*i*, *j*, and *k*, hyphae containing oidial cells, separated by empty spaces, from a culture 16 days old. × 550.—*l*, *m*, and *n*, oidial cells which have germinated. The cells were placed in a malt-wort extract three days previously. × 550.

Fig. 11.—Mycelium produced from a spore in one week in a hanging drop of meat-extract-peptone-grape-sugar-gelatine. × 550.

Fig. 12.—Germination in malt-wort extract after 24 hours. In *a* a cross-wall has been formed during the exit of the protoplasm from the spore. The protoplasm has already begun to retire from the wall; *b* was sketched one hour after *a*, and *c* two hours after *b*. The germ-tube elongated even during the retirement of the protoplasm from the wall. × 550.

Fig. 13.—Germination in malt-wort extract after 24 hours. The figure illustrates the formation of cross-walls and the retirement of the protoplasm from the spores. × 550.

Fig. 14.—Germination after three days in malt-wort gelatine. The germ-tubes are produced in various positions upon the spores. × 550.

Fig. 15.—Mycelium developed from a spore during 68 hours in 0.5 per cent. peptone. The protoplasm has crept out of the spore forming a cross-wall at its free surface during its exit. × 550.

Fig. 16.—Germ-tube from a spore, produced during 68 hours in 0.5 per cent. asparagin. Fifteen cross-walls have been formed at the free surface of the protoplasm as it crept along the germ-tube. The protoplasm is only present in a small stretch of the germ-tube near the growing point. × 550.

## Plate VII.

Fig. 17.— Similar germ-tube after 32 hours in 0.5 per cent. asparagin. × 550.

Fig. 18.—Spores after about a week in 0.01 per cent. or 1 per cent. potassium phosphate. Most of them have become multicellular, each spore having divided by one, two or three cross-walls. There is a distinct vacuole in each cell. × 550.

Fig. 19.—Spores after 14 days in tap-water. In many the protoplasmic contents have contracted, and at their free surfaces developed fresh cell-walls. Some of the spores have divided by cross-walls. × 550.

Fig. 20.—Some of the spores just described after being placed in malt-wort gelatine for 28 hours. Germination has begun. × 550.

Fig. 21.—Similar spores after 48 hours in malt-wort gelatine. × 550.

Fig. 22.—Spores left exposed on paper to the dry air of a laboratory for 14 days, viewed in water. In many of the spores fat drops have appeared. × 550.

Fig. 23.—Spores left exposed on paper to the dry air of a laboratory for 7 days, and then placed for 24 hours in malt-wort extract. Germination has begun even in the spores with large fat-drops. × 550.

Fig. 24.—Some spores described in description of fig. 22, after 42 hours in malt-wort gelatine. Germination has begun. × 550.

Fig. 25.—Generalised radial-longitudinal section corresponding to cross section described in fig. 26. The mycelium is supposed to be making its way from *R*, where the wood is in the most rotten state, to *S*, where it is still sound; *u v* and *ff* are the autumn wood cells of two successive yearly rings.

The most obvious effect of the mycelium upon the wood is seen to be the destruction of the less lignified fibres. In *h* and *i* the secondary thickening has begun to be acted upon. In *m*, *n*, *o*, and *p* the secondary thickening has almost disappeared, and the middle lamellae are in process of solution. In the region *t* the fibres have disappeared, leaving a space partly filled with hyphae. The medullary ray cells *x* to *z*, the autumn wood cells *u*, *v*, and the vessel *r*, with its surrounding cells *q* and *s*, *i.e.*, the highly lignified elements, are seen to be more persistent.

The enlargement of the pits of the medullary ray cells may be traced from *x* to *z*. The ordinary appearance of the pits on the walls of fibres is shown in *a*, *a*. Their position is usually on the radial walls. Enlarged pits which appear oval are seen in *q*, *s*, *u*, and *v*.

Holes made by hyphae through cell-walls are shown in the vessel *k*, where it will be seen they have no relation to the pits, and also in *f*, *h*, *l*, *n*, and *o*, upon radial walls, while the holes on the tangential walls in the cells *u* and *v* have been made in a similar manner.

The browning and disappearance of the protoplasm, and also the disappearance of starch grains can be traced in the medullary ray from *x* to *y*, and in the wood parenchyma and autumn wood cells from *b* to *g*.

The largest hyphae are to be seen in the freshly entered vessel *c*, the branched one having clamped connections. In the vessel *k* the hyphae are more numerous, the larger ones also with clamp-connections. In the most highly rotten wood, *q* to *w*, the hyphae are much smaller. The growth of two hyphae from the vessel *k* to the vessel *c* in straight lines perpendicular to the longitudinal axis of the fibres, is probably to be considered a chemotropic phenomenon.

In the vessel *r* a tracheal plug near the top is represented as persisting. In the same vessel are represented some curious swellings upon certain hyphae, which may possibly be oidia. × about 420.

Fig. 26.—See Pl. viii.

Fig. 27.—Hyphae of *Polyporus squamosus* with clamp-connections in a vessel.

Fig. 28.—Similar hyphae with curious cell-connections.

Fig. 29.—Piece of partition wall between two adjacent vessels covered with bordered pits; *h*, *h*, holes made by hyphae.

## Plate VIII.

Fig. 26.—Generalised transverse section to show the effect of the mycelium of *Polyporus squamosus* upon the wood of *Acer pseudoplatanus*. The mycelium is supposed to be making its way from *R*, where the wood is in the most rotten state, to *S*, where it is still sound; *e-e* and *d-d*. are the autumn wood layers of two successive yearly rings. The vessels are scattered in the spring and summer wood; *a*, *b*, and *c* are medullary rays.

The most obvious effect of the mycelium upon the wood as shown in the figure, is the destruction of the less lignified fibres in the regions *o*, *p*, *q*, *r*, and *s*, whilst the medullary ray cells, the autumn wood cells, *e-e*, and the vessels *m* and *n*, with the highly lignified layer of cells around them, have been more persistent.

The removal of the secondary thickenings, and later of the middle lamellae of the less lignified fibres, is represented near *o* and *p*.

The enlargement of the pits in the medullary ray cells will be seen by tracing down the cells from *c* to $c^1$, and similarly for the medullary rays *a* and *b*. The enlargement of the pits, which are tangential, and of the fungus holes, which are often radial, can be seen in the autumn wood cells, and is represented between *e* and *é*. A similar enlargement of pits is seen in the highly lignified cells around the vessels *m* and *n*.

The darkening and disappearance of the protoplasm in the medullary ray cells under the action of the enzymes of the mycelium can be traced from *c* to *h*. The protoplasm in the autumn wood cells *d-d*, has also become brown in colour, and is seen to be injecting the tangential pits in the cell-walls. A darkening of the protoplasm in the parenchymatous cells around the vessels *i* and *j* is also to be noted.

Tracheal plugs of apparently gummaceous consistency are shown in the vessels at *i*. In the vessel *m*, in the highly decayed wood, a tracheal plug is still seen persisting.

The hyphae of the mycelium are seen to reach their greatest diameter in the newly infected vessels *i* and *j*, whereas in the highly decayed wood, *o* to *s*, the hyphae are much thinner. Clamp-connections are to be seen upon hyphae in vessels *j*, *k*, and *m*.

The penetration of hyphae from one vessel to another, apparently in response to a chemotropic stimulus, is shown between vessels *l* and *i*, between *l* and *k*, and between *k* and *j*. × about 420.

Fig. 30.—Tangential section through rotten wood of *Acer pseudoplatanus* in the region of the autumn wood. The cells at *a*, *a*, are supposed to be more lignified, while at *b*, *b*, they are less lignified. The enlarged pits *p*, *p*, are seen on the radial walls in cross section. They are more or less hour-glass shaped. *h*, *h*, holes made by hyphae.

Fig. 31.—Radial-longitudinal section through the same wood. The cells at *a*, *a*, are supposed to be more lignified and less acted upon than those at *b*, *b*. The enlarged pits *p*, *p* on the radial walls. *h*, *h*, *h*, are holes made by a hypha and then enlarged. The destruction of the less lignified elements is represented at *b*, *b*.

Fig. 32.—Radial-longitudinal section through wood of *Acer pseudoplatanus* drawn as seen in a section. The cross-sectional view at the top of the figure is schematic and added to show distribution of the elements. *x* and *y* are two vessels. Between them are several parallel rows of holes *h*, *h*, through the intervening fibres. The hyphae which caused them are not shown. They had disappeared except at *p*, *p*. The hyphae are supposed to have grown from *x* to *y* owing to a chemotropic stimulus proceeding from the latter vessel. *t*, *t* tracheal plugs. The vessel *x* has spiral thickenings. It is divided from an adjacent vessel $x^1$ by a wall covered with bordered pits. At the back of vessel *y* are two rows of wood parenchymatous cells with pits or their walls. *a*, *a*, *a* holes made by fungus hyphae. × 250.

Fig. 33.—Cross-section through a very rotten piece of wood of *Acer pseudoplatanus* rotted by *Polyporus squamosus*. *f*, *f* where the less lignified elements have disappeared. *c-c*, *b-b*, *a-a*, the autumn wood of three successive yearly rings. *d d* a radial mycelial strand. *e* a longitudinal strand in cross-section. × 25.

Fig. 34.—A piece of very rotten wood in more detail. *a a* and *b b* autumn wood of successive yearly rings. The less lignified elements have been destroyed. The medullary rays, the autumn wood and the vessels with a layer of cells around them have persisted. × about 90.

Fig. 35.—Fibre from wood of *Acer pseudoplatanus* highly rotted by *Polyporus squamosus* and isolated by means of Schulze's maceration mixture. The pits and fungus-holes in the wall have been much enlarged by enzymes. × 300.

Fig. 36.—Similar fibre. The brown contents *c* appear to have a resinous consistency and contain air-bubbles *b*. × 300.

Figs. 37 and 38.—Contents of other fibres after treatment in the same manner as before. × 300.

## Plate IX.

Figs. 39, 40, 41, 42 and 43.—Similar fibres also isolated with Schulze's maceration mixture. *p* pits, *h* fungus-holes. × 300.

Fig. 44.—Hyphae in a vessel in very rotten wood. The mycelium is probably in a condition of starvation. × 325.

Fig. 45.—The possible reproductive bodies on the hyphae of *P. squamosus* in rotten wood of *Acer pseudoplatanus*, *a* a thick-walled hypha, *b* a thin-walled hypha with clamp-connections. × 325.

Fig. 46.—Similar swellings to those just described. × 325.

Fig. 47.—The development of the fruit-bodies of *P. squamosus*. *a*, *b*, *c* and *d*, sections through young fruit-bodies in successive stages of development showing origin of the pileus and the stipe. The stipe gradually turns upwards, so as to bring the pileus into a horizontal position. *e* and *f* side and front views of the fruit-body *b*; *g*, side view of the fruit-body *c*; *h* side view of the fruit-body *d*. *w*, *w* water drops excreted at the junction of the

stipe and the young pileus. *p*, pileus; *s*, stipe. All natural size. *i* group of the three young fruit-bodies arising from a single knob seen from above. The pilei have already become horizontal. × ½. *j*, fruit-body grown on a log for three weeks in a dark room in the Experimental Greenhouse. It is a branched stag-horn-like structure without any signs of pilei. × ⅓.

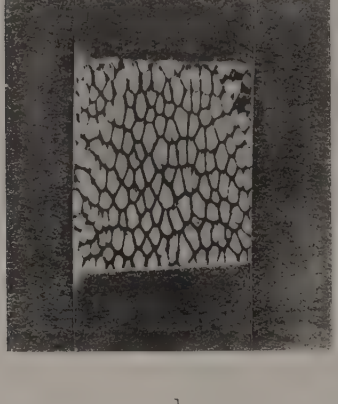
Fig. 48.—Cross-section of a fruit-body. × ½.

Fig. 49.—Pores on underside of a fully developed fruit-body. Nat. size.

Fig. 50.—Piece from the middle of a large fruit-body. Nat-size.

Fig. 51.—Hymenial layer of fruit-body showing basidia with sterigmata and spores. × 360.

Journ. Econ. Biology, 1906, Vol. 1, pt 3.



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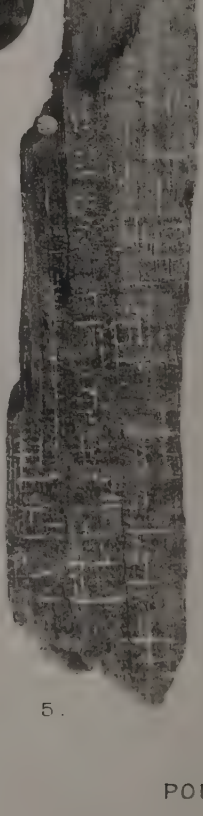
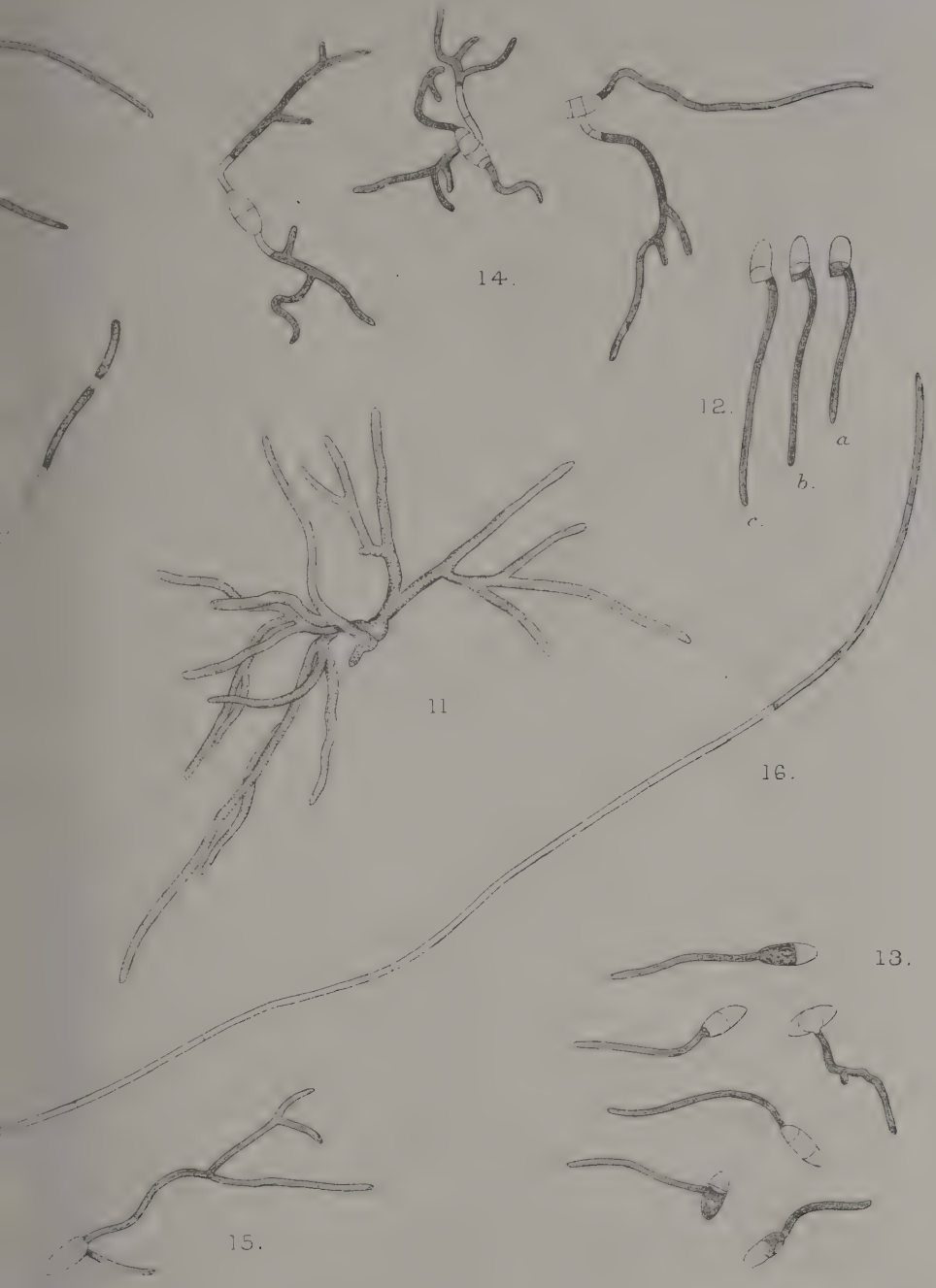


5.

POLYPORUS

MOSUS, Huds.

Huth London

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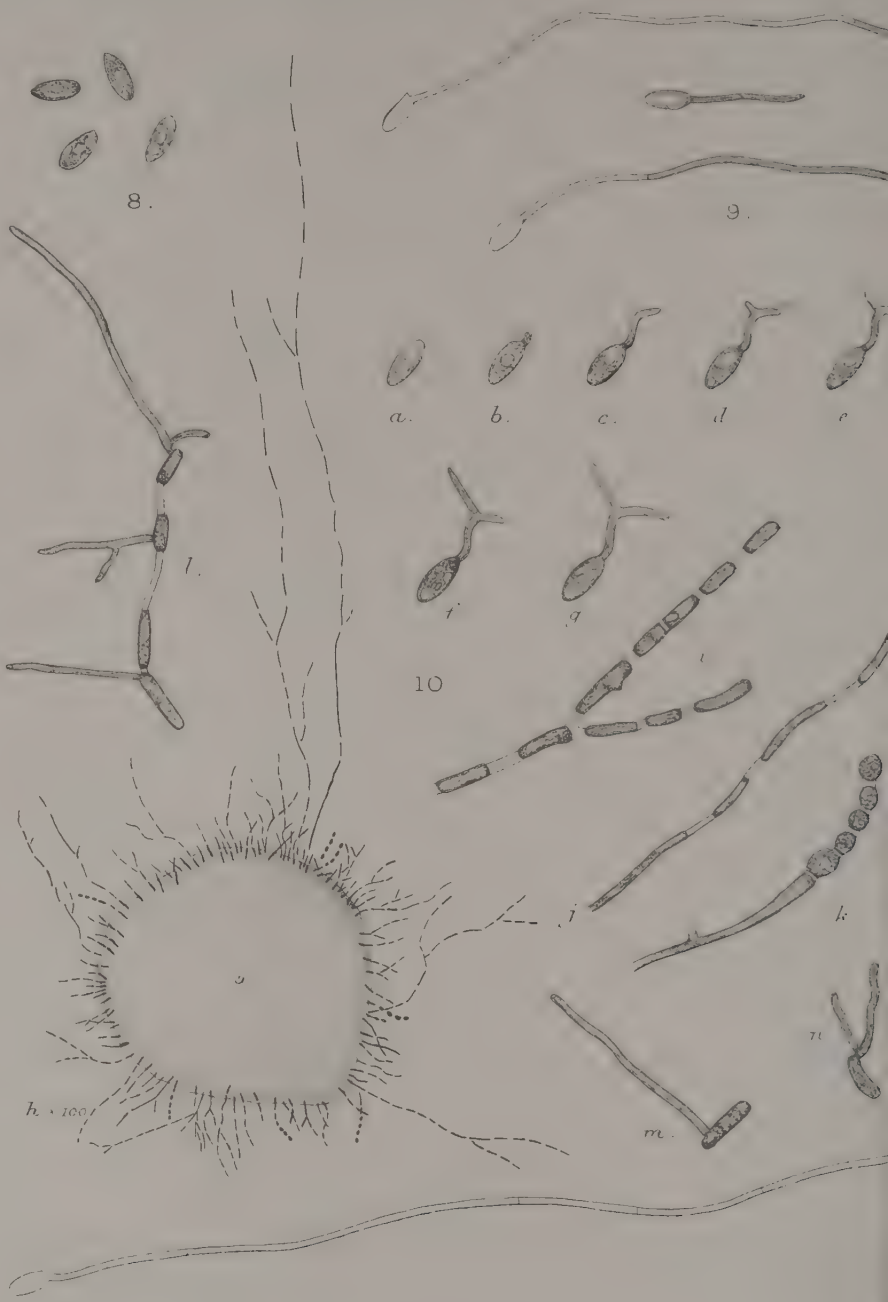
AMOSUS, Hud.

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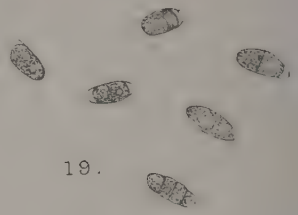

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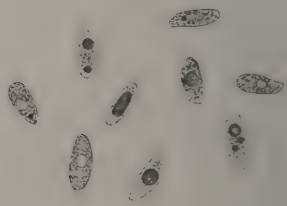

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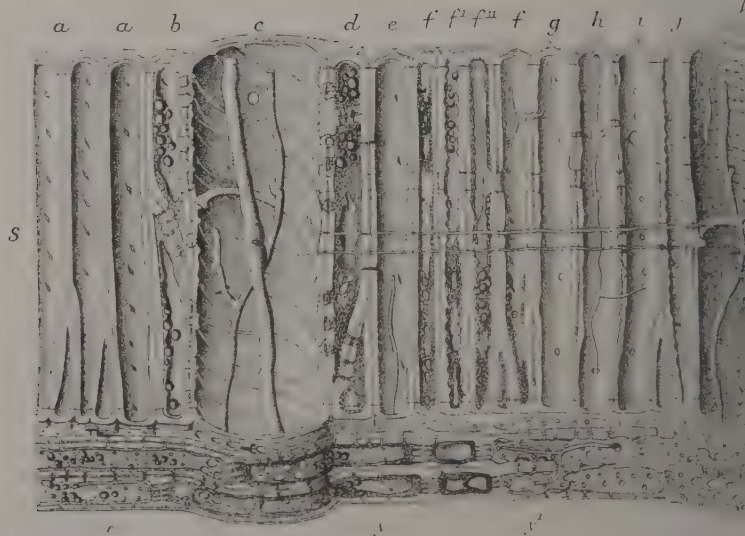


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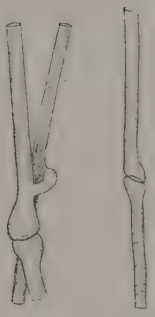

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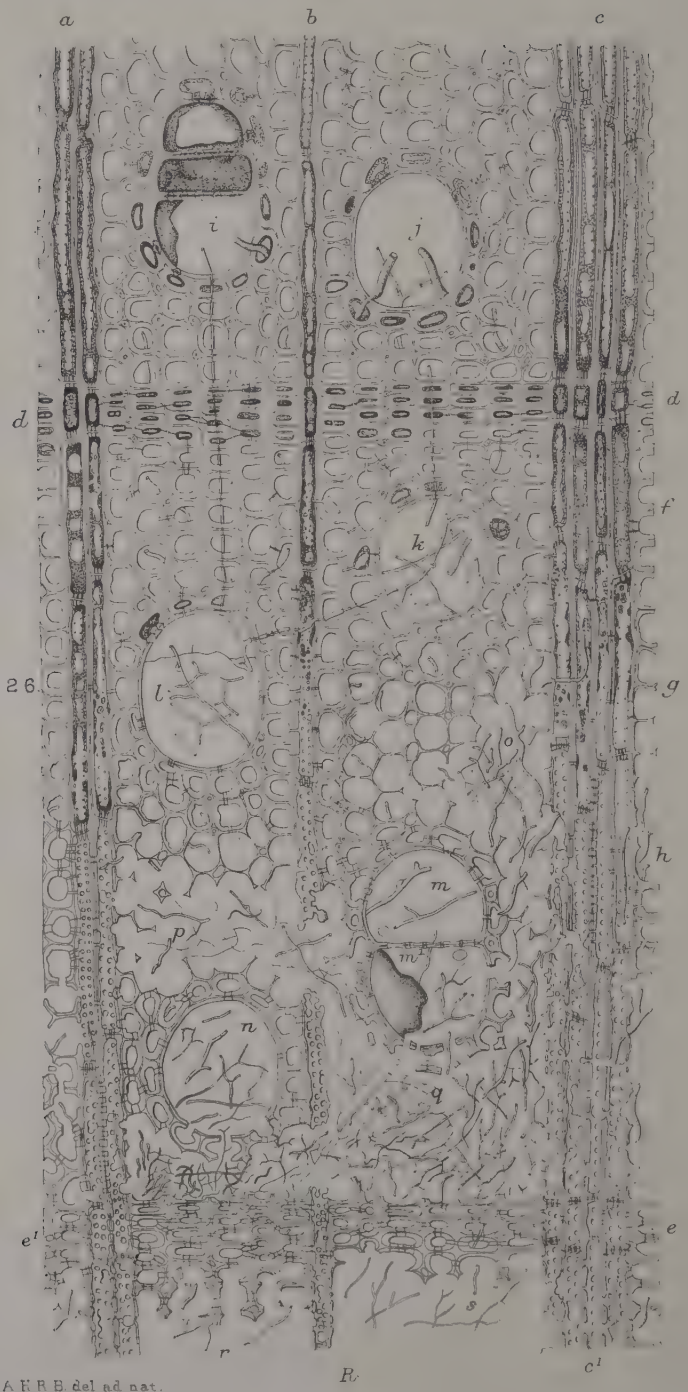


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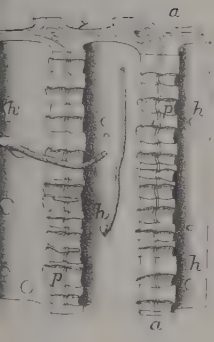


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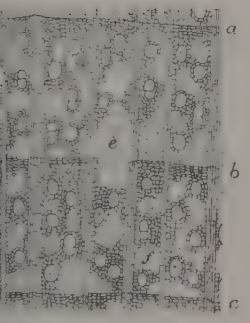


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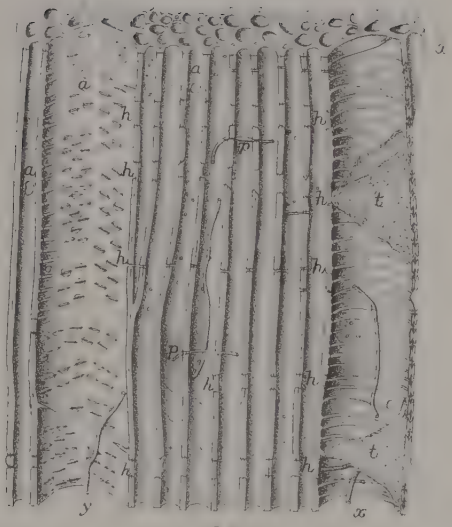


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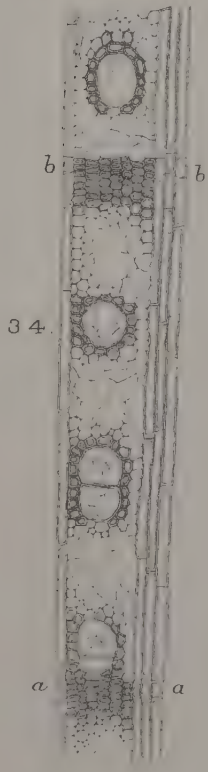


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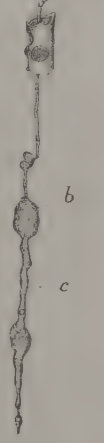


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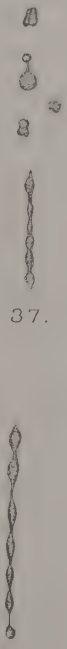

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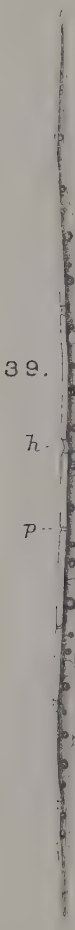

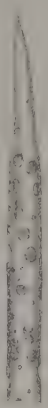


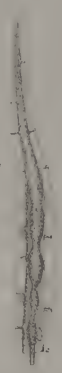


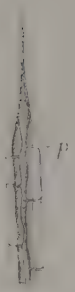


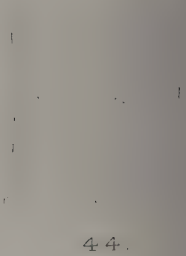


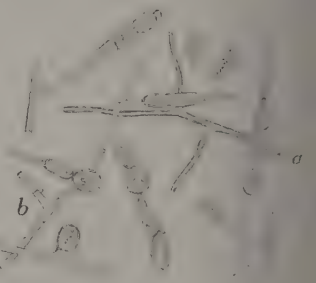


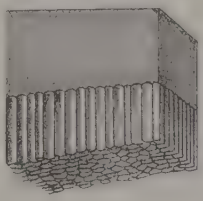


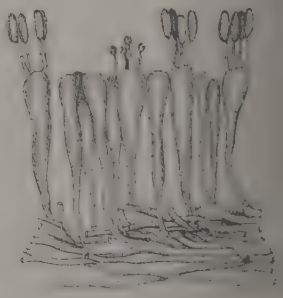


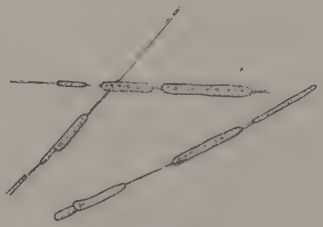

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Huth, Lith^r London.

SUS. Huds.